이학석사 학위논문

A juvenile ornithopod-dominated tracksite from the Lower Cretaceous Haman Formation, South Korea

한국의 하부 백악기 함안층에서 발견된 아성체 조각류 발자국 화석지에 대한 연구

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윤 한 상

ABSTRACT

A new dinosaur tracksite with footprints of non-adult ornithopods was discovered from the Lower Cretaceous Haman Formation (Albian), Gunbuk District, Haman County, South Gyeongsang Province of South Korea in 2018. The tracksite (33 m^2) consists of 55 ornithopod footprints (six short trackways and 27 isolated footprints) within three track-bearing horizons partially exposed on the small creek bottom. Lithofacies and sedimentary structures of the track-bearing horizons and overlying strata suggest a marginal lacustrine environment. All tracks are sub-symmetrical tridactyl and small- to medium-sized pes prints. They have wide, blunt, short digital impressions with a large, rounded heel pad impression. No manus print is observable in the tracksite. Tracks are generally longer than their width with a distinctly developed digit III. Trackways show the inward (negative) rotation of footprints. The morphological characteristics of the footprints are most likely attributable to ichnogenus *Caririchnium*. Relatively small pes size (lengths range from 13 to 27 cm) indicates that the trackmakers were juvenile to subadult ornithopods compared with the contemporary large ornithopods in Korea. The majority of the trackways show preferred orientations with trends of parallel to subparallel groupings on each horizon, suggesting gregarious behavior. Notably, the tracksite consists exclusively of juvenile ornithopod dinosaurs, which is an uncommon phenomenon compared to other ornithopod tracksites with age-mixed or large ornithopod footprints frequently found in the world. The absence of the adult ornithopod tracks would be interpreted as the spatial segregation of ornithopod population based on their ages and the formation of the juvenile-only community without parental care.

Keywords: Footprints, *Caririchnium*, Juvenile dinosaurs, Ornithopod, Early Cretaceous, Haman Formation, Haman County, South Korea

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INTRODUCTION

Since dinosaur footprints were discovered for the first time in the Upper Cretaceous Jindong Formation in early 1980's (Yang, 1982), South Korea has been noteworthy for numerous and diverse Cretaceous vertebrate ichnocoenoses (Lockley et al., 2012a). They include a variety of vertebrate trace fossils such as turtles, lizards, crocodyliforms, dinosaurs, birds, pterosaurs, and mammals from the non-marine Cretaceous Gyeongsang Basin and other small sedimentary basins (Lee et al., 2000, 2001; Hwang et al., 2002; Huh et al., 2003, 2006; Lockley et al., 2006, 2012b, c, 2020; Kim et al., 2016; Lim et al., 2012; Kim and Lockley, 2016; Kim et al., 2017a, b; Lee et al., 2018a). However, the first vertebrate ichnological study in South Korea began with Kim (1969)'s bird track report on *Koreanaornis hamanensis* from the Lower Cretaceous Haman Formation.

The Haman Formation belongs to the Hayang Group of the Cretaceous Gyeongsang Basin (Chang, 1975). It has produced various vertebrate trace fossils such as birds, pterosaurs, theropods, and sauropods (Kim, 1969; Baek and Yang, 1997; Kim et al., 2006, 2008, 2012a,b; Falk et al., 2010, 2014; Kim et al., 2011; Kim and Lockley, 2012), but ornithopod tracks are relatively rare compared to their abundant trackways from the overlying Jindong Formation (Lee et al., 2000; Kim and Huh, 2018), thereby detailed ichnological information of ornithopods in this period of time are insufficient (Huh et al., 2003; Park and Lim, 2004; Yang et al., 2006). Fortunately, a new ornithopod tracksite was discovered from the Haman Formation located at a small valley in Gunbuk District, Haman County, South

Gyeongsang Province in 2018 (Fig. 1). The exposed surface of the outcrop is small (33 m^2 in total) but consists of a high density of footprints. Interestingly, they are all small tridactyl footprints attributable to the juvenile ornithopod dinosaurs as trackmakers. Therefore, the purpose of this paper is to report and describe this new ornithopod tracksite from the Lower Cretaceous Haman Formation, and to investigate the paleontological and paleoecological importance of this tracksite.

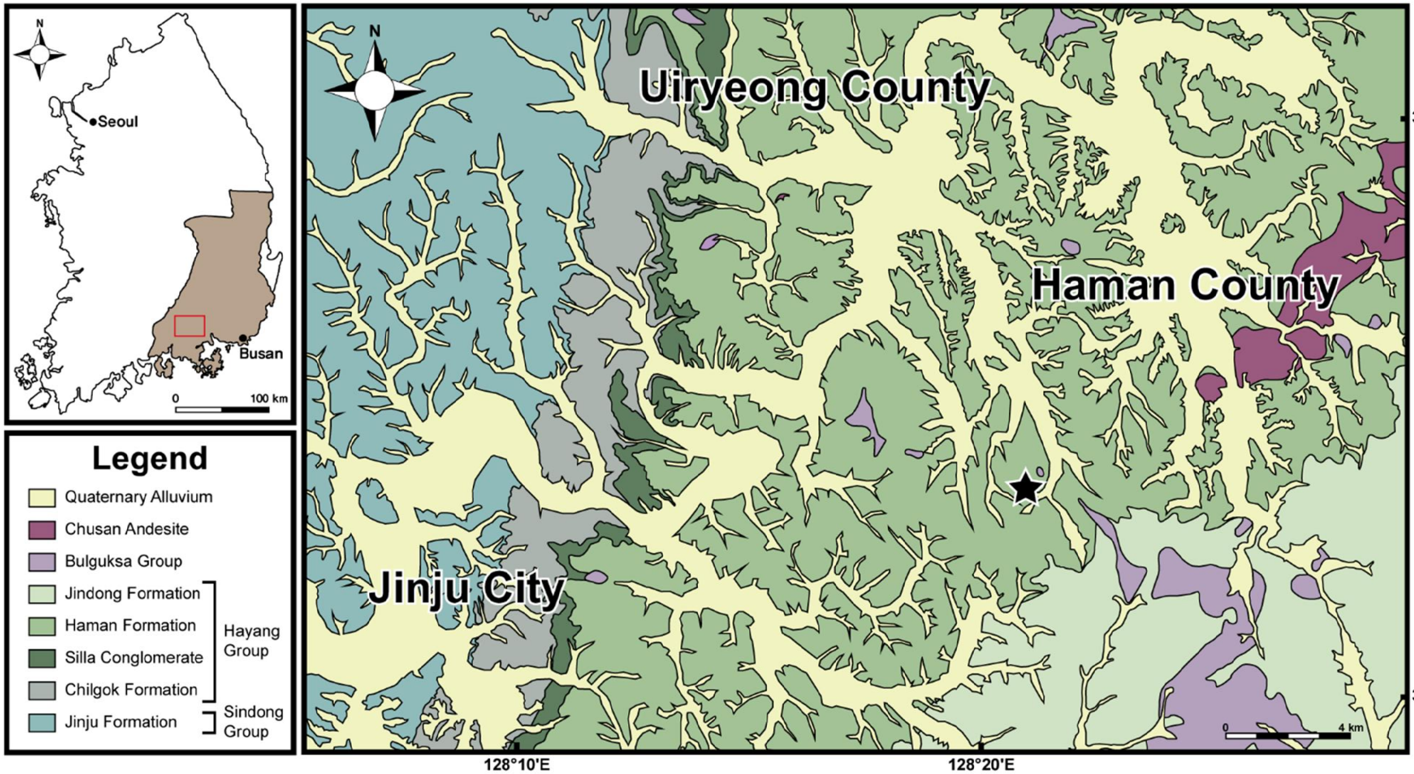

FIGURE 1. Geological map of the study area and the locality of tracksite (Modified from Choi and Kim, 1963; Lee et al., 2018b). Brown region of the southern Korean peninsula (left upper) refers to the Gyeongsang Basin and the red square refers to the region of geological map (right). Black star in the geological map refers to the locality of tracksite.

GEOLOGICAL SETTING

The Gyeongsang Basin is the largest terrestrial sedimentary basin in South Korea located at the southeastern part of the Korean peninsula. It is interpreted as a backarc basin formed by the oblique subduction of the proto-Pacific (Izanagi) plate under the Asian continent (Chough and Sohn, 2010). The sedimentary beds of the Gyeongsang Basin are grouped as the Gyeongsang Supergroup, and subdivided into three major lithostratigraphic units: the Sindong, Hayang, and Yucheon groups in ascending order (Chang, 1975).

The Haman Formation belongs to the middle to upper part in the Hayang Group (Chang, 1975) and lies between the underlying Silla Conglomerate and overlying Gusandong (Kusandong) Tuff with thicknesses ranging between 500-2600 m (Chough and Sohn, 2010). The Haman Formation is distributed over the Jinju subbasin and the Daegu area of Uiseong subbasin. In the Jinju subbasin, the Jindong Formation overlies the Gusandong Tuff and the Haman Formation while the Banyaweol Formation overlies the Gusandong Tuff and the Haman Formation in the Daegu area (Chough and Sohn, 2010). The Haman Formation is typically characterized by the occurrence of purple mudstone and sandstone (Um et al., 1983) and generally interpreted to be deposited in alluvial or fluvial settings with a semi-arid climate (Kim, 1969; Chough and Kim, 2010; Paik and Kim, 2014). In some regions where the upper Haman Formation occurs, the typical reddish deposits are absent, and instead, lacustrine lithofacies formed by cyclic depositions of gray sandstone and mudstone with intercalating calcrete-bearing deposits have been reported, showing similar aspect to the general lithofacies of the overlying Jindong Formation (So et al., 2007; Kim et al., 2018).

The new tracksite is represented by three track-bearing layers (Layer 1, 2, 3 from top to bottom) partially exposed on the small creek bottom (Figs. 2, 3). All layers consist of dark gray mudstone with polygonal fractures on the surface. Between the upper two track-bearing layers (Layer 1 and 2), there is another layer exposed without any tracks (Layer A). This trackless layer contains symmetrical ripple marks which are not preserved in other track-bearing layers (Fig. 2E). The ripples occur in the southwestern part of Layer A with azimuths of 120°. The Layer 1 (15 cm thick) and Layer A come into the direct contact and the Layer 2 is next to the Layer A (4-5 cm thick) with a small groove between them. The Layer 3 locates about 6 m southwest from the Layer 2 (40 cm thick). Besides the track-bearing layers, reddish sandstone and mudstone beds overlie the track-bearing horizons. Two lithofacies (dark gray mudstone and reddish sandstone to mudstone) alternate in the section along the creek (Fig. 3). Wavy bedding and symmetrical ripple marks are observed from the lower section of reddish sandstone. In general, the sedimentary strata gently dip towards the southeast at an angle around 5°. Besides the dinosaur tracks, no fossils are found from the track-bearing layers except for cylindrical rhizoliths (6 to 8 mm in diameter) developed parallel to the bed in form of horizontal branching network (Fig. 2B). The alternating lithofacies with the typical sedimentary structures such as wavy bedding, symmetrical ripple marks, and rhizoliths indicate that the tracksite was deposited in a marginal lacustrine environment with fluctuating water level (Reineck and Wunderlich, 1968; Cohen, 1982; Paik and Chun, 1993).

There have been several reports of vertebrate ichnofossils from the Haman Formation. The bird tracks are the most abundant trace fossils (Baek and Yang, 1998; Kim et al., 2006, 2012a; Falk et al., 2010, 2014; Kim et al., 2011). Other tracks are pterosaurs (Kim et al., 2006, 2012b), theropods (Kim et al., 2008), and sauropods (Kim and Lockley, 2012). Recently, well-preserved sole skin impressions of sauropod dinosaurs have also been reported (Paik et al., 2010, 2017). Although there are some reports about ornithopod footprints from the Haman Formation (Huh et al., 2003; Park and Lim, 2004; Yang et al., 2006), they all have never been studied in detail.

The maximum depositional ages of the Haman Formation and the overlying Jindong Formation were dated to be 105.4 ± 0.4 Ma and 99.9 ± 0.7 Ma, respectively by a recent U-Pb analysis of detrital zircons using SHRIMP and MC-ICPMS (Lee et al., 2018b). The Gusandong (Kusandong) Tuff is a key bed which is distributed over a wide range (~200 km) between the Haman and Jindong formations. The eruption ages of the northern and the southern Gusandong Tuff (NKT and SKT) are 103.0 ± 1.2 Ma and 104.1 ± 1.3 Ma, respectively by a SHRIMP U-Pb analysis (Kim et al., 2013). Since the boundary between the Lower and Upper Cretaceous places in 100 Ma (Walker et al., 2013), the Haman Formation corresponds to the late Albian.

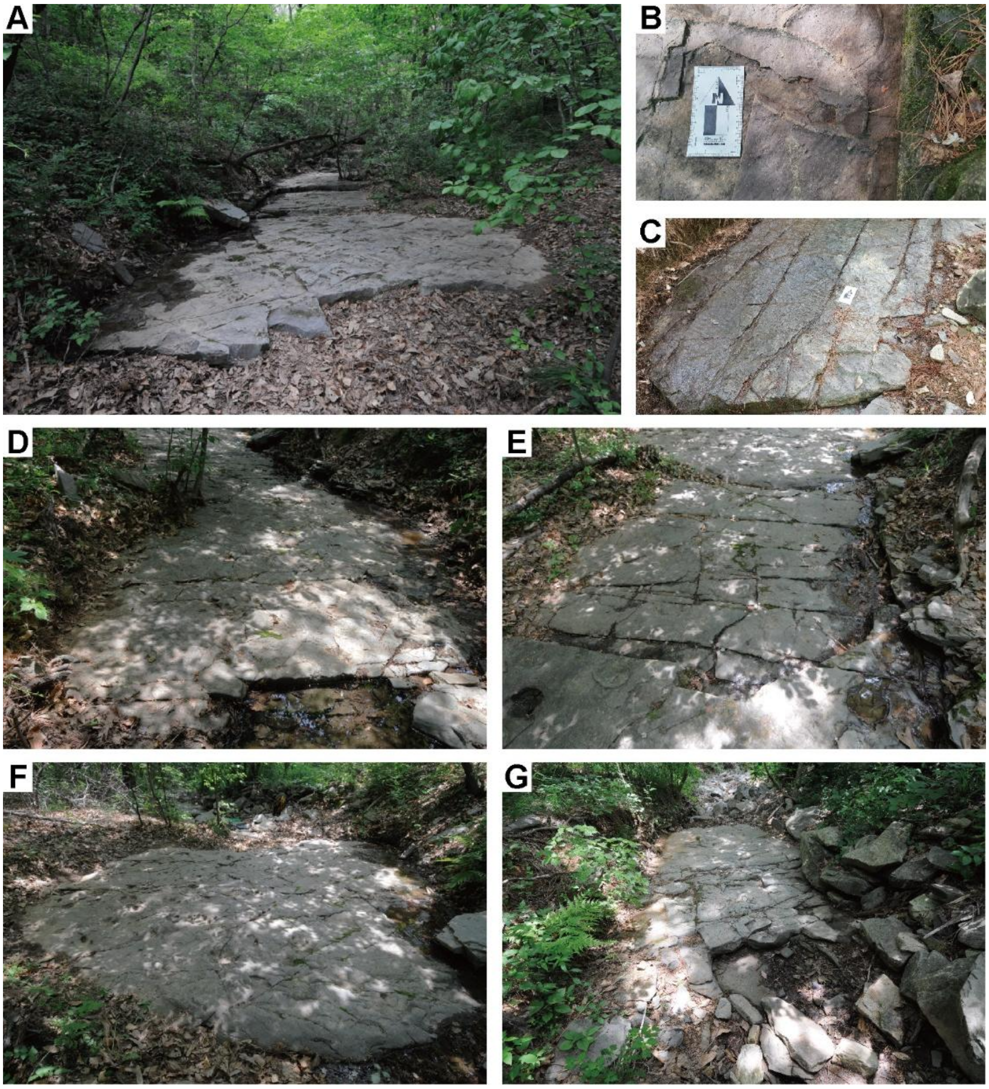

FIGURE 2. Photos taken from the Gunbuk dinosaur tracksite. A) General view of Gunbuk dinosaur tracksite showing Layer 1, Layer A and Layer 2 in descending order. B) Branching network of rhizolith from the overlying strata. C) Ripple marks shown from the overlying strata. D) Track-bearing Layer 1. E) Layer A with partially preserved symmetrical ripple marks. F) Track-bearing Layer 2. G) Track-bearing Layer 3.

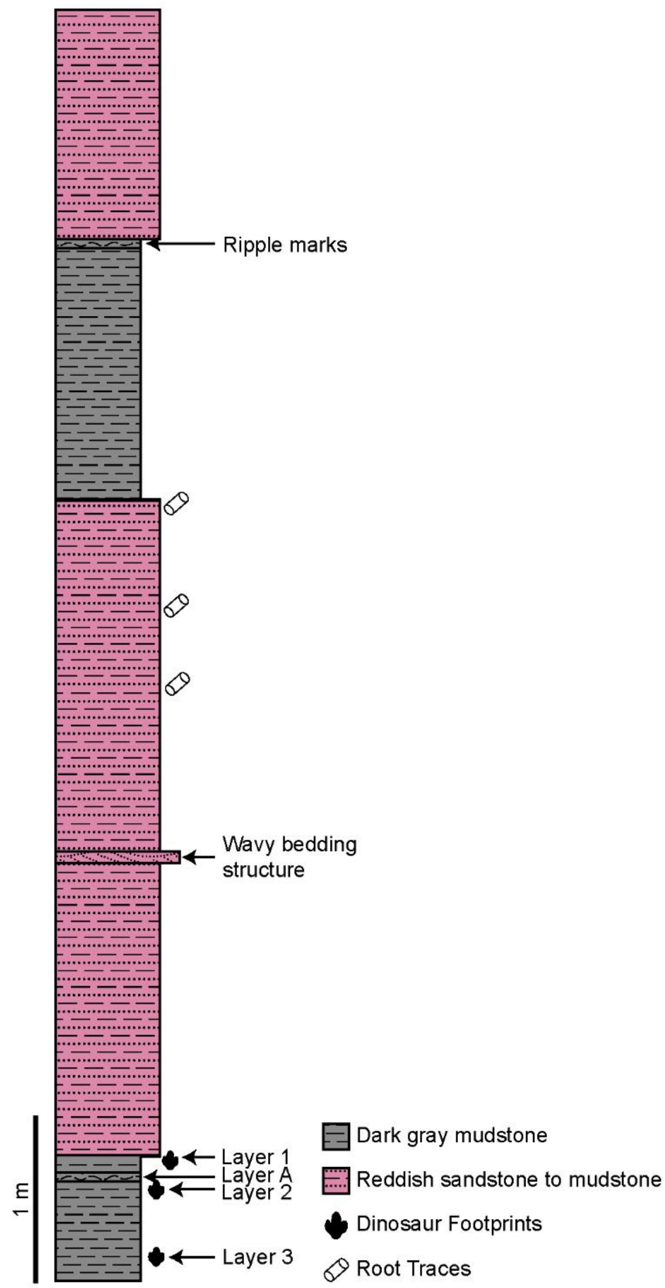

FIGURE 3. Columnar section of the sedimentary strata of Gunbuk tracksite.

METHODS

The exposed surface was digitally mapped using the photogrammetry to obtain the 3-D images of the whole track-bearing layers and to get the close-up images of the best-preserved footprints. Digital photogrammetry requires photos of the subject from various angles taken from the calibrated digital camera and the software for data processing (Kong et al., 2010). The camera and the data processing software used in this study are Nikon D300 and Agisoft Photoscan (Metashape) Standard version. After producing a single 3D model and a point cloud of each layer, ply file was exported for further treatment using another data processing software. Cloudcompare version 2.10-beta was used to resize the model and match the actual tracksite with the elimination of the unnecessary part and to obtain the contour data of each footprint and the whole tracksite. Outline drawings of the tracks and tracksite were drawn using the combination of contour map and image of the tracksite through Adobe Illustrator.

Terminology used here follows the work of Lockley (2009), Castanera et al. (2013), and Lee et al. (2018c). Measurements were taken for the footprint length (L), footprint width (W), the ratio of footprint length and width (L/W), length of digits (II, III, IV), divarication angles between digits II and III (D(II-III)), and digits III and IV (D(III-IV)), the ratio between the anterior triangle length and width (AT l/w), the stride length (SL), pace length (PL), pace angulation (ANG), the azimuth of track (azimuth), and track rotation inside trackway (TR). The measurement procedures of Lockley (2009) and Castanera et al. (2013) were modified and used for tracks and trackways (Fig. 4). The midpoint of the distal end of the digit III was set as a reference point for measurement because digit III imprints show good preservation in most tracks unlike heel pad impression or other parts of footprints. Measurements of the footprints were made using Adobe Illustrator from the line drawings. Measurement of the surface area of the outcrops was made through the software ImageJ. Rose diagram of the azimuth of tracks was plotted using the software GeoRose version 0.5.1.

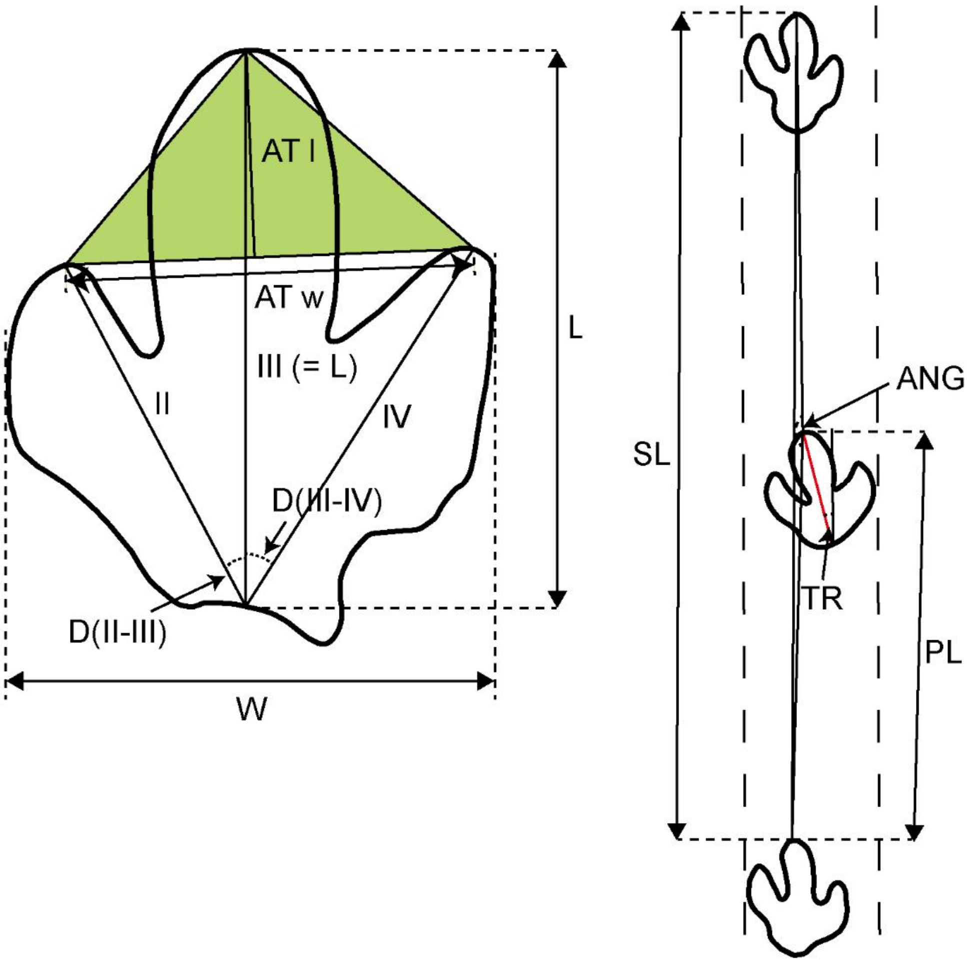

FIGURE 4. Measurements taken from the individual tracks and the whole trackway (modified from Castanera et al., 2013). Green triangle refers to the anterior triangle of the track. Abbreviations: L = footprint length; W = footprint width; II = digital length of digit II; III = digital length of digit III (= L); IV = digital length of digit IV; AT l = anterior triangle length; AT w = anterior triangle width, D(II-III) = divarication angle between digits II and III; D(III-IV) = divarication angle between digits III and IV; SL = stride length; PL = pace length; ANG = pace angulation; TR = track rotation.

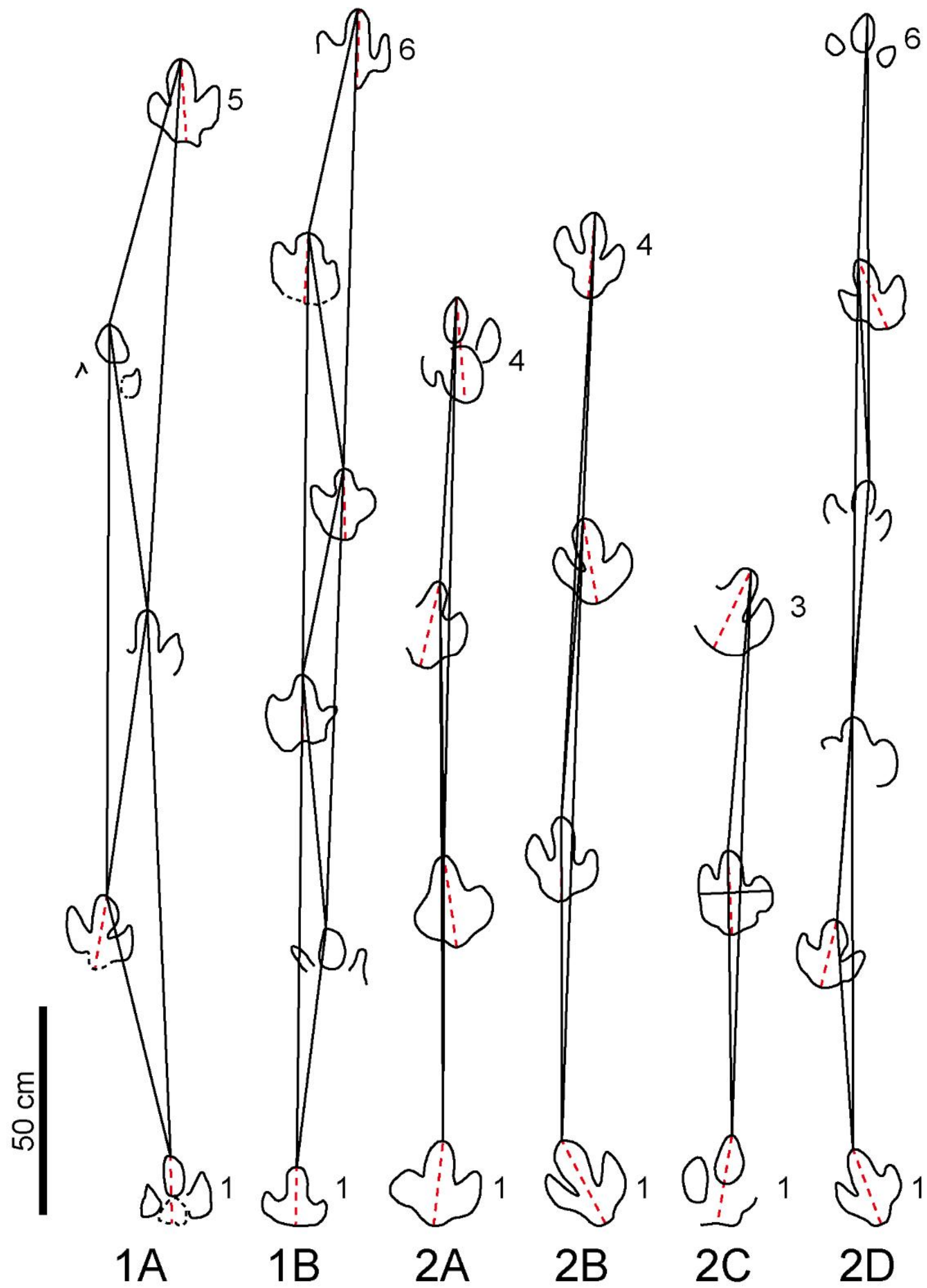

FIGURE 5. Outline drawings of six trackways from the Gunbuk dinosaur tracksite.

Scale = 50 cm.

TABLE 1. The average value of six ornithopod trackways from Gunbuk tracksite. Abbreviations are aforementioned in Methods. Measurements of lengths are done in cm.

Trackway	L	W	L/W	II	III	IV	D(II-III)	D(III-IV)	Azimuth	SL	PL	ANG	AT l/w
1A	17.8	17.0	1.05	12.7	17.8	15.1	29.8	31.4	143.4	133.8	67.3	159.9	0.50
1B	16.6	16.4	1.01	12.7	16.6	13.6	36.2	30.7	141.4	111.3	56.3	163.1	0.37
2A	22.2	20.4	1.05	15.3	22.2	17.2	29.3	29.3	33.3	134.1	67.6	177.6	0.52
2B	20.9	17.8	1.18	15.9	20.9	17.1	26.4	26.6	123.8	147.5	74.4	177.0	0.41
2C	20.8	17.7	1.14	17.5	20.8	16.0	20.1	28.4	39.6	135.9	68.0	174.5	0.32
2D	17.9	16.0	1.13	14.1	17.9	13.6	30.6	31.6	136.5	107.9	54.6	174.9	0.40
Average	19.4	17.5	1.09	14.7	19.4	15.4	28.7	29.7	-	128.4	64.7	171.2	0.42

SYSTEMATIC ICHNOTAXONOMY

Superorder Dinosauria Owen, 1842.

Order Ornithischia Seeley, 1888.

Suborder Ornithopoda Marsh, 1881

Ichnofamily Iguanodontipodidae Vialov, 1988 *sensu* Lockley, Xing, Lockwood and Pond, 2014, emend. Diaz-Martinez, Pereda-Suberbiola, Perez-Lorente and Canudo, 2015.

Diagnosis. Mesaxonic, tridactyl, subsymmetrical pes tracks that are wide as or wider than long; one pad impression in each digit and one in the ‘heel’; digit pads longer than wide; well-developed notches in the proximal part of the digit II and IV impressions; manus tracks occasionally present and much smaller than the pes tracks.

Ichnogenus *Caririchnium* Leonardi, 1984, emend. Diaz-Martinez, Pereda-Suberbiola, Perez-Lorente and Canudo, 2015.

Type ichnospecies *C. magnificum* Leonardi, 1984.

Diagnosis. Pes tracks belonging to Iguanodontipodidae, with a large ‘heel’ impression that is rounded, centered and wide (wider than the width of the proximal part of the digit III impression); short, wide digit impressions.

Caririchnium isp.

Material. Fifty-five tracks from Gunbuk tracksite. Pes-only natural mold.

Horizon and locality. Dark gray mudstone, the upper part of the Haman Formation, Lower Cretaceous (Albian); Sachon-ri, Gunbuk District, Haman County, South Gyeongsang Province, Korea.

Description. Tridactyl pes 12.9 – 26.8 cm long (average 18.7 cm). Footprint length longer than wide in most tracks (average L/W ratio 1.09). Tracks exhibit relatively developed digit III with an average AT l/w ratio of 0.43 (See Appendix).

The best-preserved track (Track 1A-5) is longer than its width with the L/W ratio of 1.14. The separation between three digital impressions and a 'heel' impression is not well-preserved. The 'heel' pad (metatarsophalangeal impression) is rounded with subtriangular distal part. The width of digit III is slightly narrower than its 'heel' pad but wider than those of digits II and IV. Also, the digit III is longer than digits II and IV, and the digital IV imprint is more shallowly impressed than digital II and III imprints. The distal ends of digits are blunt. Track 1A-5 is a part of trackway 1A from Layer 1 that consists of five consecutive pes tracks, showing bipedal locomotion (Fig. 5). Trackway 1A exhibits average stride and pace lengths of 133.8 cm and 67.3 cm, respectively (Table 1).

Except for Layer A, 55 footprints were mapped and measured from three track-bearing layers (Fig. 6-8). Six trackways consisting of 28 footprints were identified on Layers 1 (1A, 1B) and 2 (2A-2D) along with 27 isolated footprints from three track-bearing layers (Fig. 5). Footprints on Layer 3 are all isolated tracks. All tracks show positive depressions of sizes ranging from 12.9 cm to 26.8 cm with an average of 18.7 cm in length (Fig. 9). Among the trackways, the trackway 1B consists of the smallest footprints with an average 16.6 cm in length while the largest ones with an average 22.2 cm in length belong to the Trackway 2A. Due to the limited exposure of the outcrop surface, all trackways from the Gunbuk tracksite consist of only three to six consecutive footprints.

The track-bearing layers are located at the bottom of a small creek where the stream flows, so tracks must have been continuously washed out since subaerial exposure. Therefore, most of the tracks are supposed not to show detailed morphologies due to the eroded surface of track-bearing layers. Nevertheless, some tracks are exceptionally well-preserved without big deformation. No manus tracks are observed in this tracksite. Pes prints are tridactyl with subsymmetrical outline, showing wide and short digits with blunt distal ends. Tracks do not show distinct claw marks (Figs. 10-13). Most tracks are longer than wide or similar in length and width. The L/W ratio varies from 0.89 to 1.30 (average 1.09) with one peculiar exception of 1.61 (Fig. 9). Nonetheless, the average L/W ratios of tracks are relatively consistent in the trackways, ranging from 1.01 to 1.18 (average 1.09; Table 1). The average divarication angle between digits II-III (D(II-III)) and digits III-IV (D(III-IV)) are 28.7° and 29.7°, respectively. However, the average D(II-III) of trackways are more inconsistent than D(III-IV), ranging from 20.1° (Trackway 2C) to 36.2° (Trackway 1B) (Table 1). The average anterior triangle ratio (AT l/w) of tracks is 0.43, showing that digit III is relatively enlarged than other digits. All tracks of the trackways show an inward (negative) rotation (mostly within 12°), but several tracks show greater rotation than 20°.

The pace and stride lengths of all trackways vary from 54.6 cm and 107.9 cm (Trackway 2D) to 74.4 cm and 147.5 cm (Trackway 2B), respectively. The pace angulation ranges from average 159.9° (Trackway 1A) to 177.6° (Trackway 2A) with an average 171.2°. Although half of the footprints are isolated and somewhat randomly distributed, the azimuths of tracks are quite concentrated around 120° to 150° (Fig. 14). Two trackways in Layer 1 (1A, 1B) show the average azimuths of 143.4° and 141.4°, showing almost parallel orientation while those of four trackways in Layer 2 (2A, 2B, 2C, 2D) are 33.3°, 123.8°, 39.6°, and 136.5°, respectively. Trackways on the Layer 2 are concentrated in two directions that show near perpendicular orientation to each other (2A and 2C vs 2B and 2D).

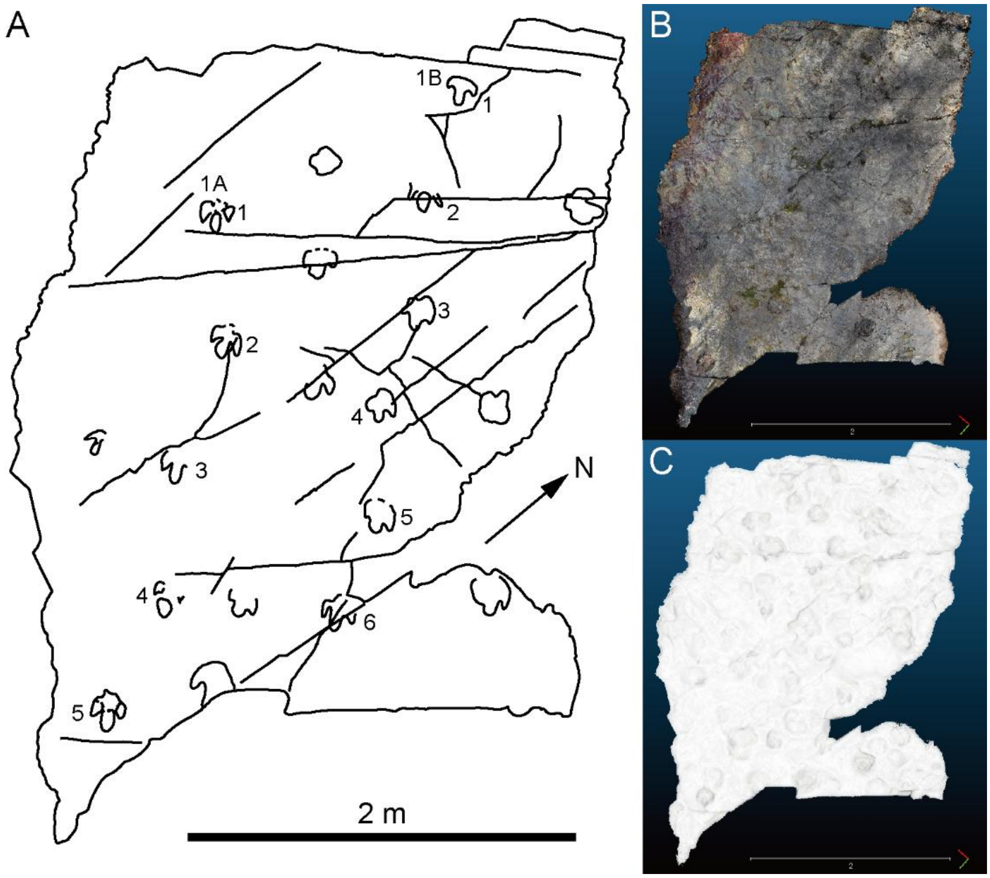

FIGURE 6. Map of the Layer 1 from Gunbuk tracksite. A) Line drawing as a schematic map (scale = 2 m). B) Image of the 3D photogrammetric model of the layer reconstructed by data processing software. C) Shaded image of the 3D photogrammetric model.

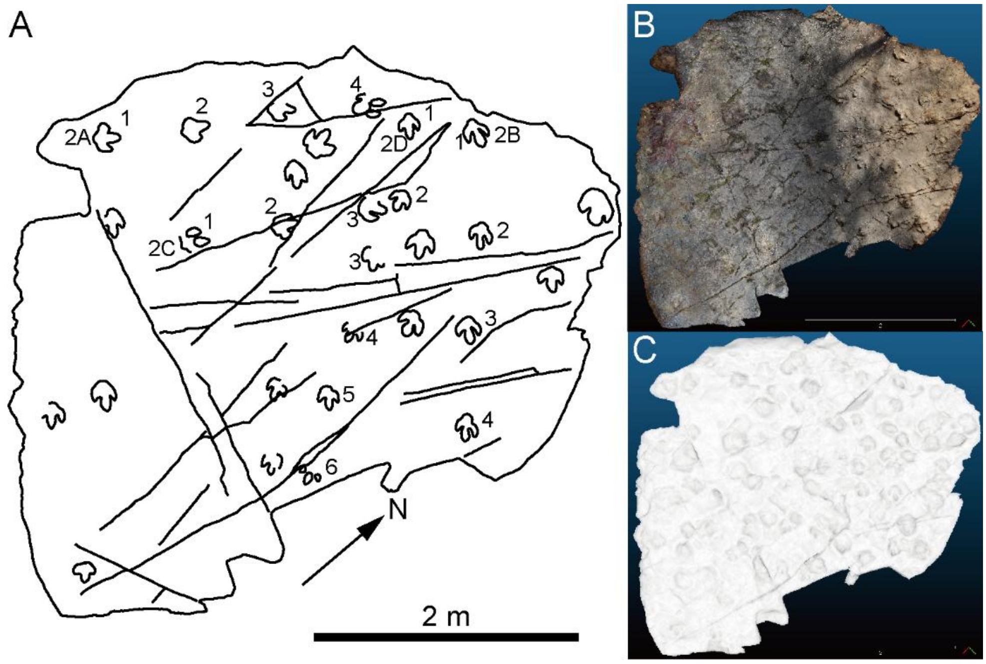

FIGURE 7. Map of the Layer 2 from Gunbuk tracksite. A) Line drawing as a schematic map (scale = 2 m). B) Image of the 3D photogrammetric model of the layer reconstructed by data processing software. C) Shaded image of the 3D photogrammetric model.

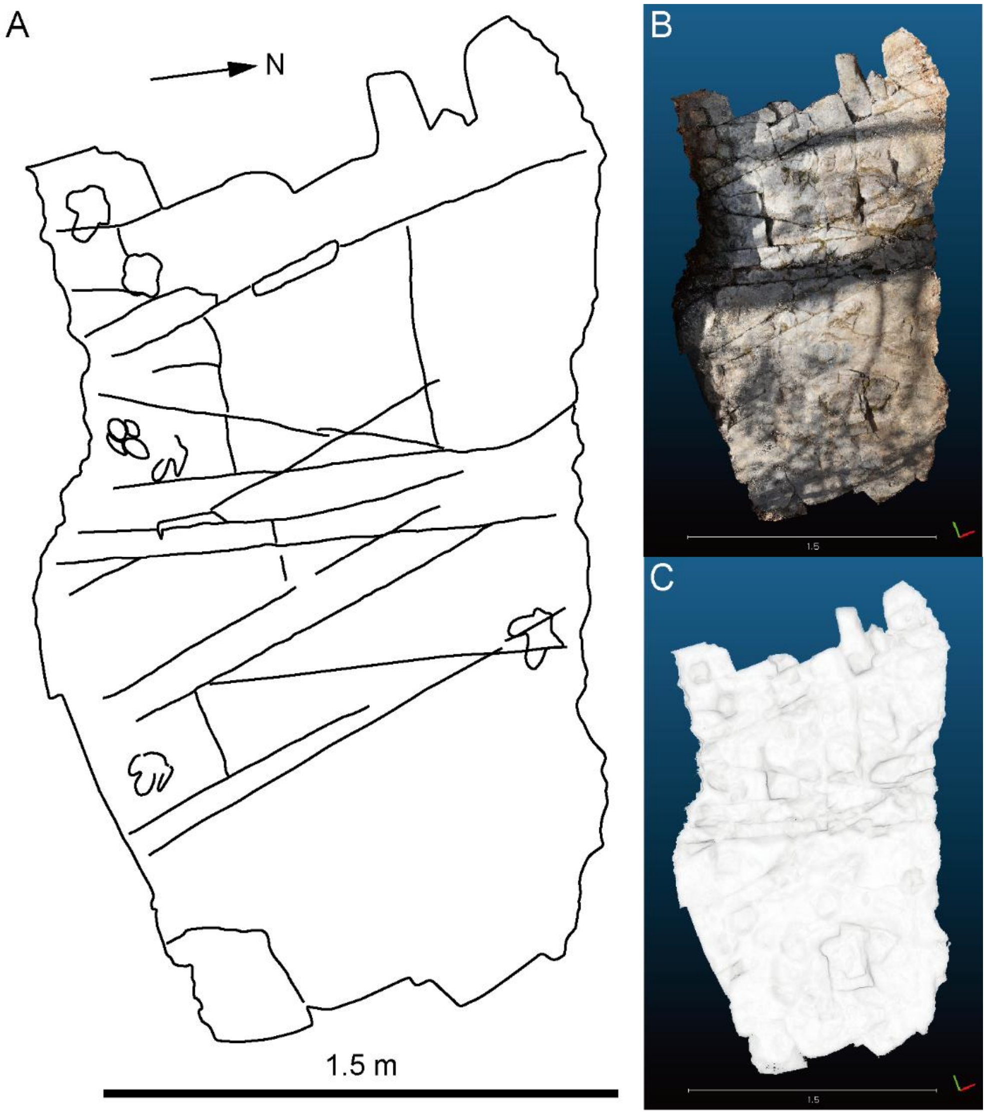

FIGURE 8. Map of the Layer 3 from Gunbuk tracksite. A) Line drawing as a schematic map (scale = 1.5 m). B) Image of the 3D photogrammetric model of the layer reconstructed by data processing software. C) Shaded image of the 3D photogrammetric model.

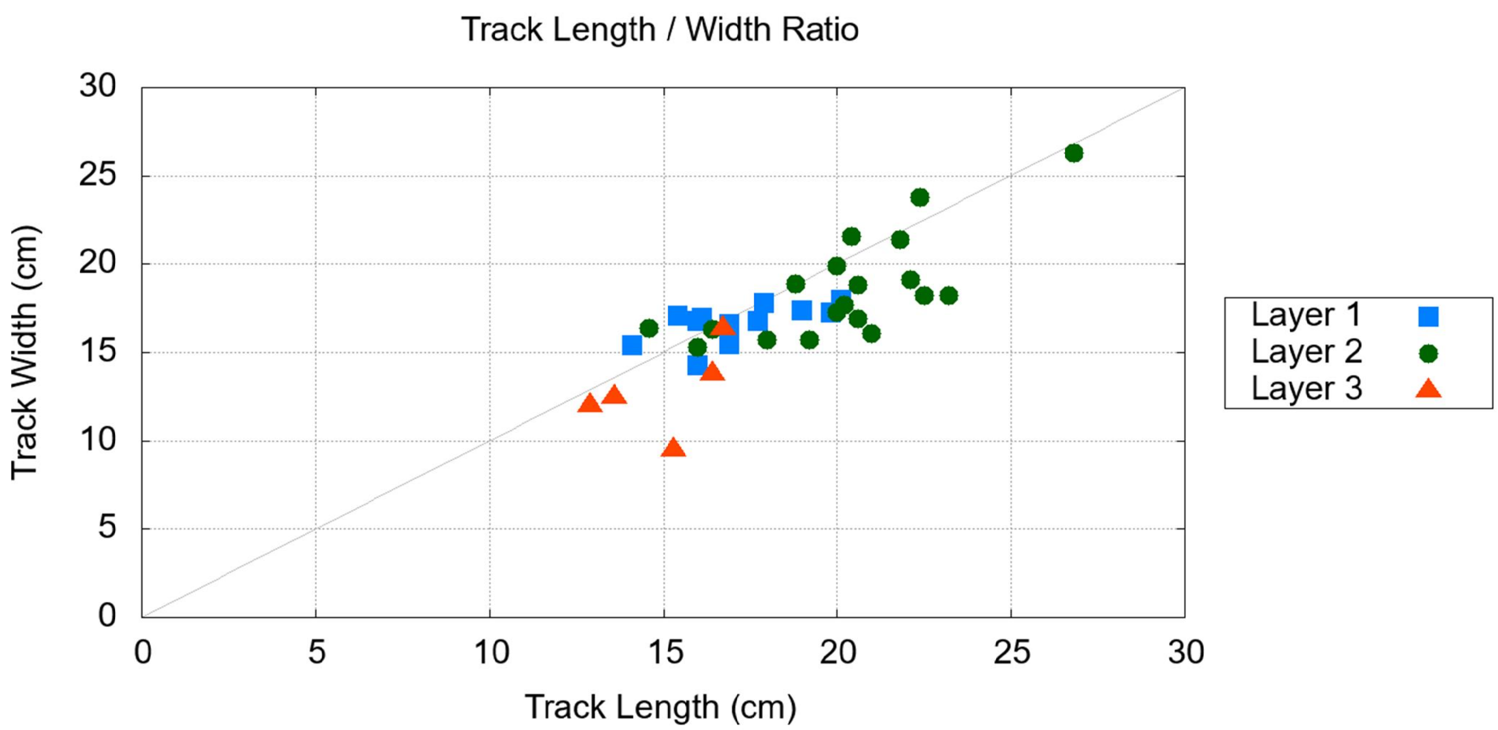

FIGURE 9. The ratio between track length and track width from Gunbuk tracksite.

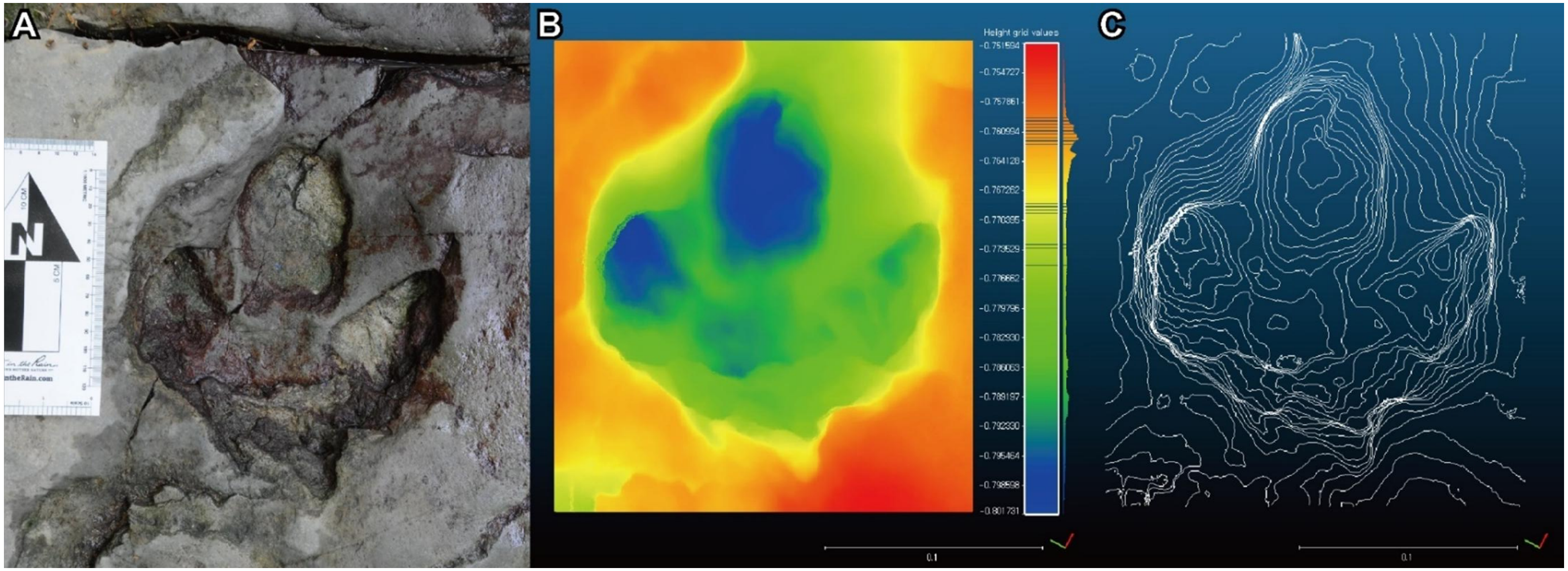

FIGURE 10. Images of the track 1A-5. A) Photograph of the real footprint. B) 3D photogrammetric false-color depth map.

C) Contour map (2 mm interval). Scales of B and C = 10 cm.

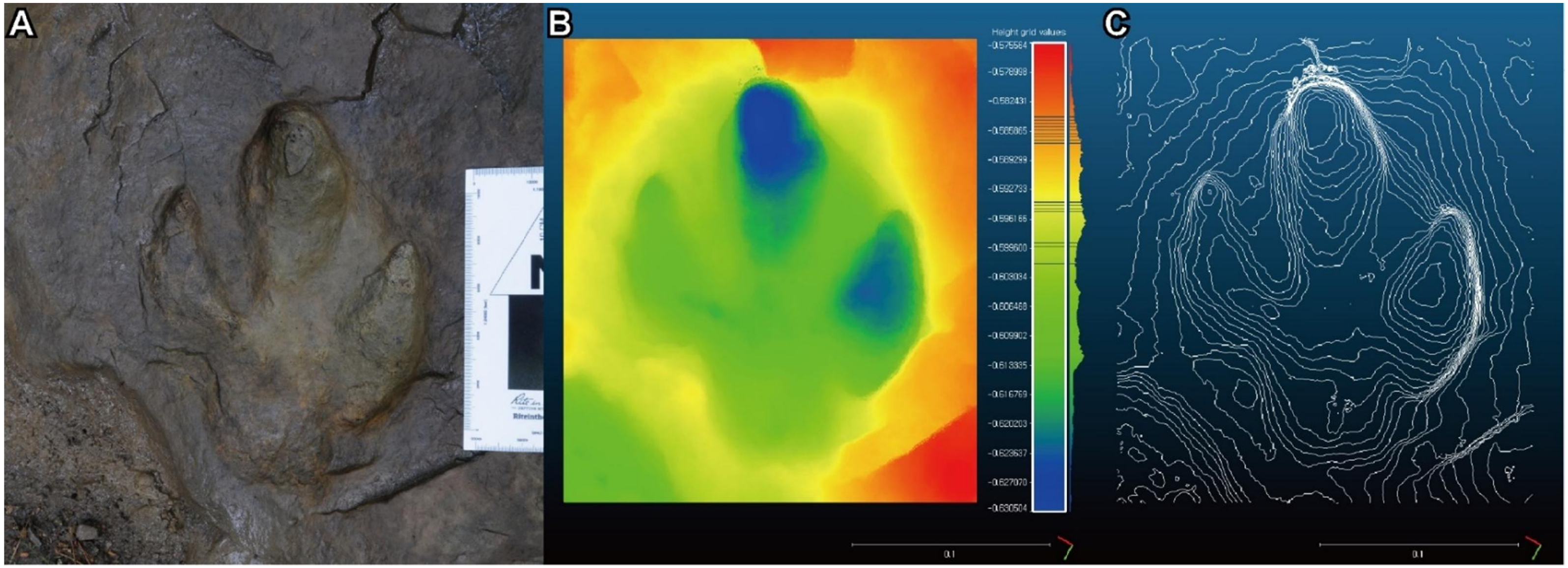

FIGURE 11. Images of the track 2B-1. A) Photograph of the real footprint. B) 3D photogrammetric false-color depth map. C) Contour map (2 mm interval). Scales of B and C = 10 cm.

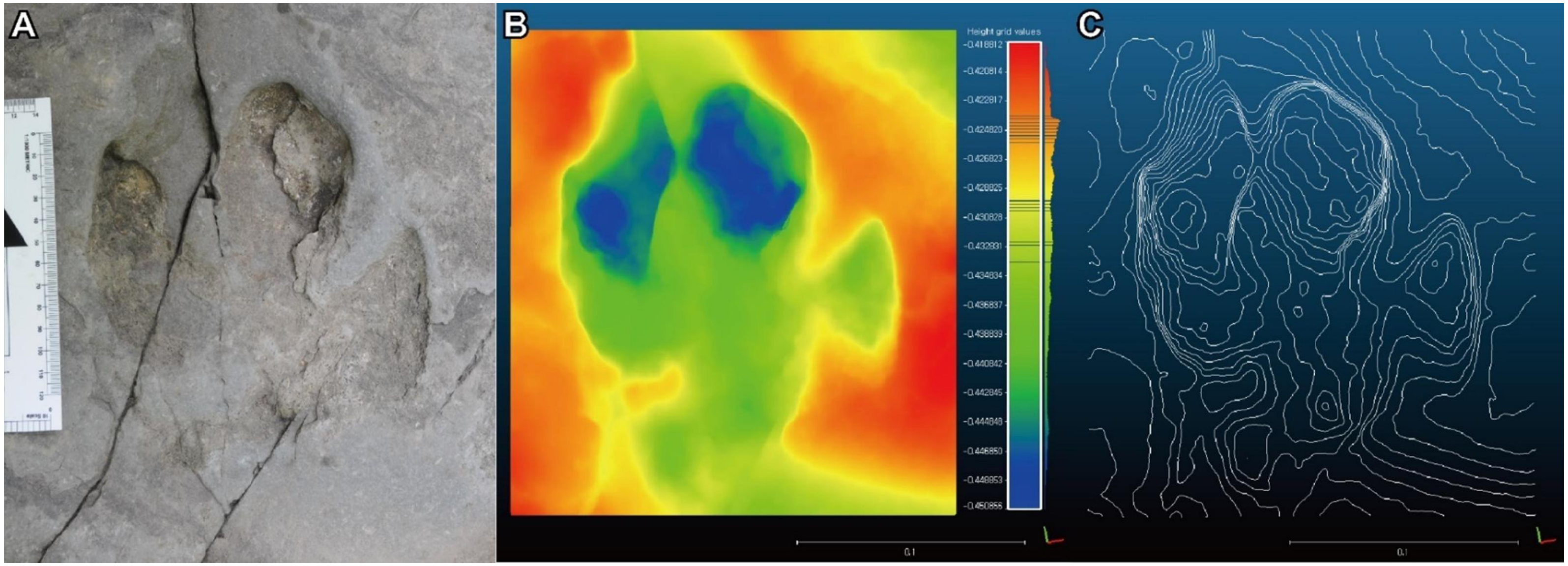

FIGURE 12. Images of the track 1A-2. A) Photograph of the real footprint. B) 3D photogrammetric false-color depth map. C) Contour map (2 mm interval). Scales of B and C = 10 cm.

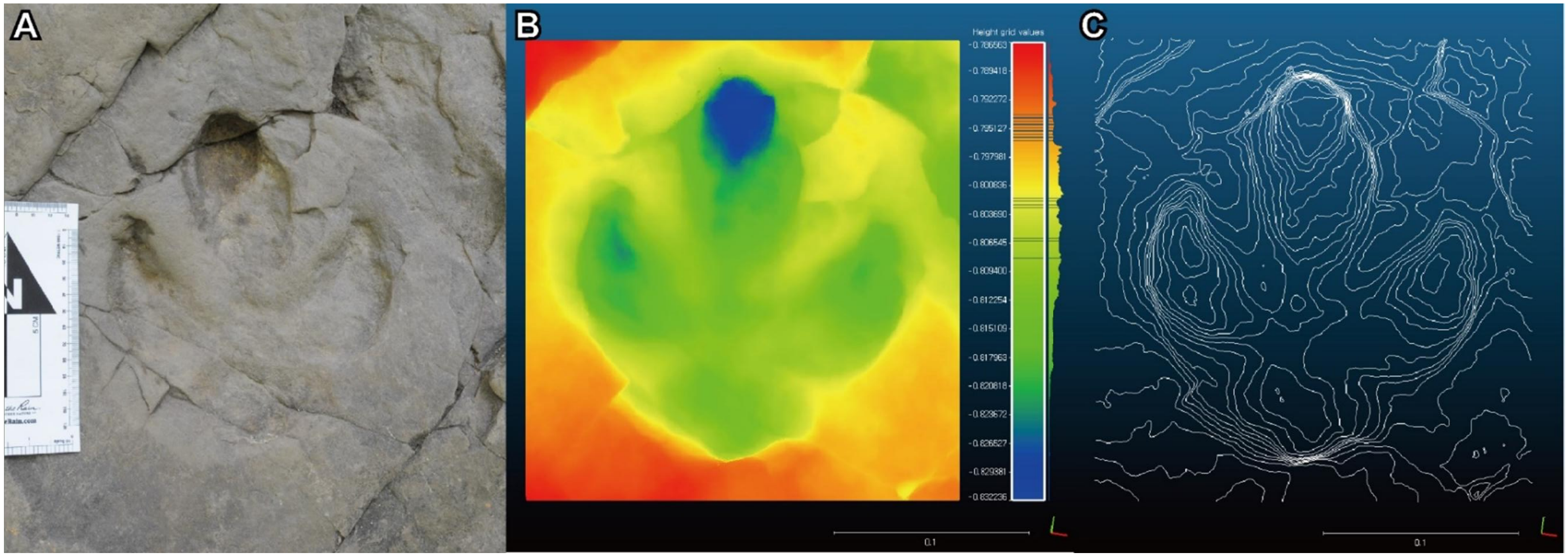

FIGURE 13. Images of the track 2B-3. A) Photograph of the real footprint. B) 3D photogrammetric false-color depth map. C) Contour map (2 mm interval). Scales of B and C = 10 cm.

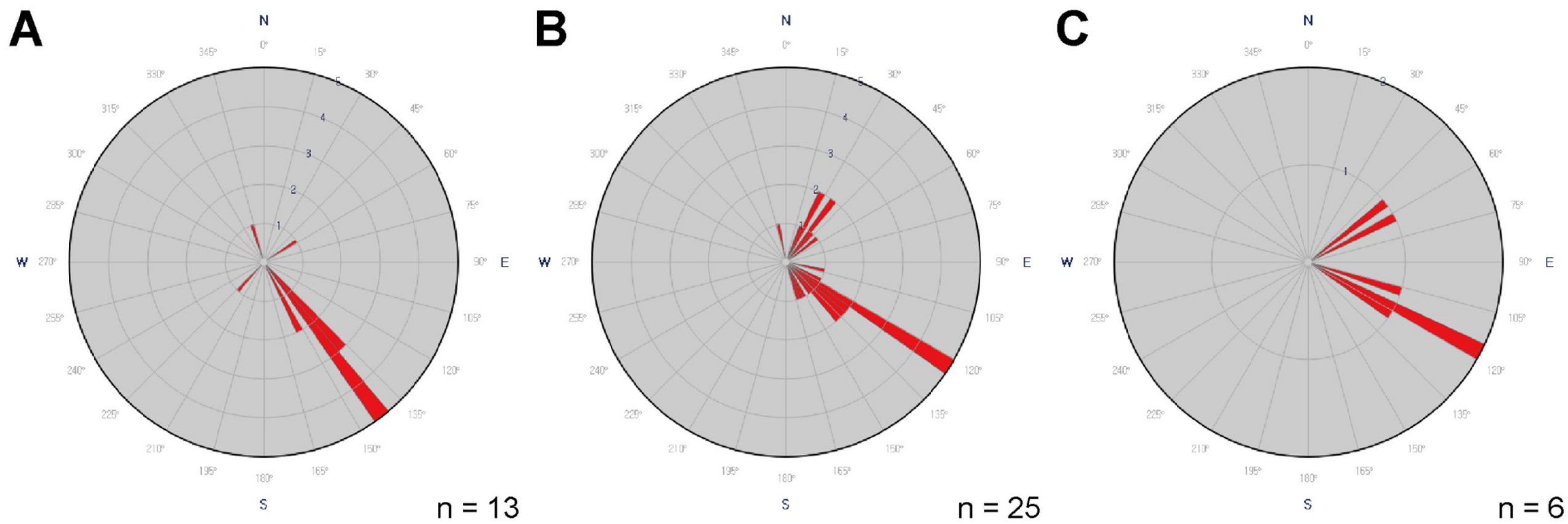

FIGURE 14. Rose diagrams plotting the azimuths of tracks from the Gunbuk dinosaur tracksite. n refers to the number of the measured tracks. A) Layer 1. B) Layer 2. C) Layer 3.

DISCUSSION

Possible trackmaker

All footprints are subsymmetrical tridactyl pes tracks, which can be interpreted as theropod or ornithopod tracks (Castanera et al., 2013). In general, theropod pes prints show larger L/W ratio with narrower and longer digits than those of ornithopod footprints because theropods had the acuminate distal end of digits with sharp claws while ornithopods had the blunt distal end of digits and a rounded metatarsophalangeal impression (Moratalla et al., 1988). All morphological characteristics of the Gunbuk tracks indicate that the trackmakers were ornithopods rather than theropods. Moreover, the strong negative rotation of tracks is one of the key characters of ornithopod dinosaurs (Moratalla et al., 1992).

Considering only the footprint size, small basal Early Cretaceous neoornithischians such as jeholosaurids and parksosaurids might be possible candidates of the trackmaker. However, their tracks are more gracile than those of larger and derived ornithopods, having relatively slender and long digits with claw marks (Thulborn, 1994; Olsen and Rainforth, 2003; Gierlinski et al., 2009). Most of the tracks from this tracksite have wide and short digits with the blunt distal end without claw marks, suggesting that more derived ornithopods with blunt toes are more reasonable to be considered as potential trackmakers.

Lee and Lee (2007) reported a maxillary tooth from the Lower Cretaceous Hasandong Formation (Aptian) that belongs a derived iguanodontoid. Likewise, a derived iguanodontian *Fukuisaurus* and a basal hadrosauroid *Koshisaurus*

(Kobayashi and Azuma, 2003; Shibata and Azuma, 2015) were discovered from the Lower Cretaceous Kitadani Formation (Aptian), Japan. Besides, a non-hadrosaurid iguanodontian *Equijubus* (You et al., 2003) was also reported from the Gongpoquan Basin (late Early Cretaceous), Gansu Province, China. In Albian age, a derived iguanodontid *Altirhinus* (Norman, 1998) and basal hadrosauroids like *Probactrosaurus* (Rozhdestvensky, 1967; Norman, 2002) or *Penelopognathus* (Godefroit et al., 2005) have been reported from Mongolia and Inner Mongolia, China. Considering the temporal and paleogeographical distribution, the trackmakers of the Gunbuk tracksite were most likely attributable to derived iguanodonts or basal hadrosauroids.

Comparisons to Cretaceous ornithopod ichnotaxa in East Asia (Fig. 15)

In South Korea, Cretaceous ornithopod tracks are mainly discovered from the Late Cretaceous Jindong Formation of Gyeongsang Basin, South Gyeongsang Province (Lee et al., 2001; Huh et al., 2003; Lockley et al., 2006; Kim and Huh, 2018), including two ichnotaxa *Ornithopodichnus masanensis* (Kim et al., 2009) and *Caririchinium kyoungsookimi* (Lim et al., 2012). However, Diaz-Martinez (2015) declared *O. masanensis* as a nomen dubium and emended *C. kyoungsookimi* as *Hadrosauropodus kyoungsookimi*. Tracks originally reported as *Ornithopodichnus* were robust and slightly wide tridactyl tracks with weakly developed digit III (Kim et al., 2009; Lockley et al., 2012b, 2014), which differ from Gunbuk ornithopod tracks. *H. kyoungsookimi* tracks are diagnosed with small manus prints and large pes prints with bilobed 'heel' impressions, which is also different from pes-only Gunbuk tracks with rounded 'heel' impressions. On the other hand, the Early Cretaceous ornithopod tracks have been reported from isolated small sedimentary basins in South Korea. *Caririchnium yeongdongensis* (Kim et al., 2016) reported from the Lower Cretaceous Sainri Formation (Valanginian-Hauterivian) of the Yeongdong Basin, North Chungcheong Province has pes prints similar to Gunbuk tracks, but its diagnoses are mainly based on the characteristics of manus prints, thereby meaningful comparisons to Gunbuk tracks are hard to be achieved. In other cases, *Caririchnium*-type tracks discovered from the Lower Cretaceous Sanbukdong Formation of Gunsan City, North Jeolla Province also have morphological similarity to those of Gunbuk tracks in general

(Lee et al., 2018c). Unfortunately, detailed comparisons are difficult due to the poor preservation of tracks.

Tsukiji et al. (2018) reported ornithopod footprints from Lower Cretaceous Kitadani Formation (Aptian) and classified them as *Caririchnium* isp. and *Amblydactylus* isp. mainly based on their L/W ratio and 'mesaxony' of tracks. Pes prints of *Caririchnium* isp. are similar to those of Gunbuk tracks showing high AT l/w ratio (average 0.43) indicating that digit III is relatively enlarged than other digits, but Kitadani tracks include manus impressions occasionally. Unlike *Caririchnium* tracks, *Amblydactylus* tracks are wider than its length with low AT l/w ratio (average 0.27), which differ from Gunbuk tracks. Other ornithopod tracks from the Lower Cretaceous Tetori Group have been also reassigned as *Caririchnium* and *Amblydactylus* recently (Tsukiji et al., 2019).

Ichnotaxonomically, Gunbuk tracks well correspond to the diagnosis of ichnogenus *Caririchnium*, such as the wide and short, blunt digits and rounded 'heel' pad impression that is wider than the proximal part of digit III impression (Diaz-Martinez et al., 2015; Xing et al., 2015). All other ichnospecies but *C. lotus* from the Jiaguan Formation (Barremian-Albian), China exhibit tracks longer than its width (Xing et al., 2007, 2015). At the ichnospecies level of *Caririchnium*, the 'heel' pad impression longer than wide was used as an autapomorphic character of *C. lotus* (Xing et al., 2007, 2015; Diaz-Martinez et al., 2015). Notably, ornithopod trackways discovered from the Lower Cretaceous Sanbukdong Formation have been recently suggested to be very similar to pes imprints of *C. lotus* in that respect (Lee et al., 2018c). However, Gunbuk tracks show the morphological and preservational variation of the metatarsophalangeal dimension. Therefore, it is reasonable to conclude that they are assigned to *Caririchnium* isp.

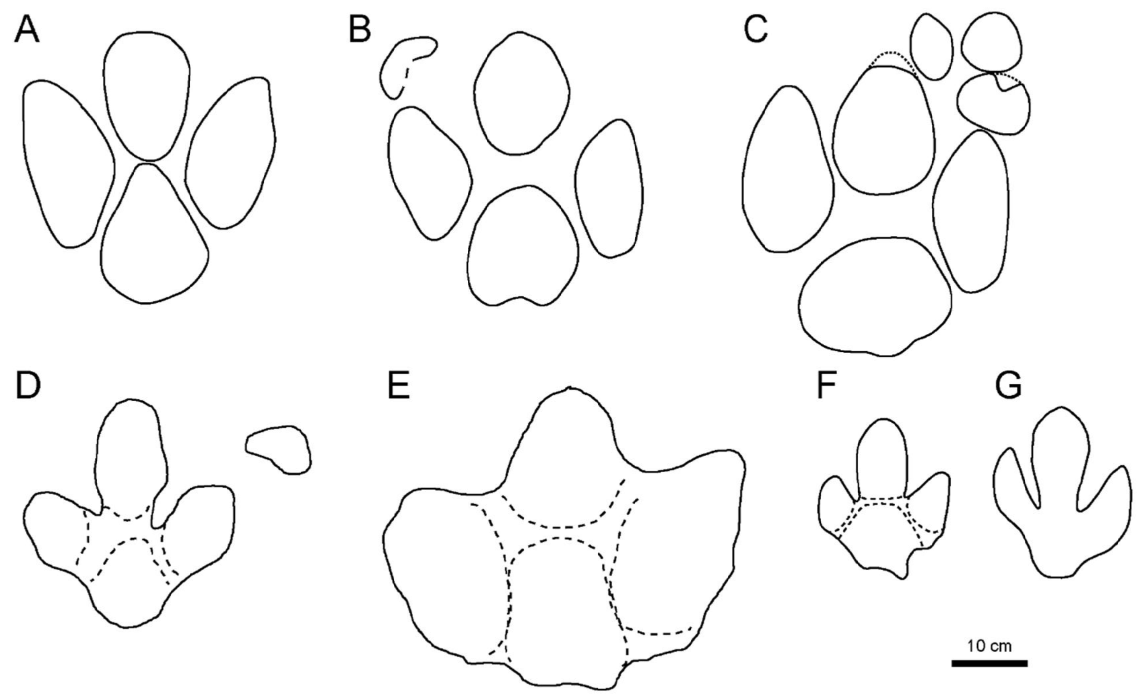

FIGURE 15. Comparison between large ornithopod ichnogenera of East Asia and the best-preserved footprints of the Gunbuk tracksite. A) *Caririchnium lotus* (redrawn from Xing et al., 2007). B) *Hadrosauropodus kyoungsookimi* (redrawn from Lim et al., 2012). C) *C. yeongdongensis* (redrawn from Kim et al., 2016). D) *C.* isp. (redrawn from Tsukiji et al., 2018). D) *Amblydactylus* isp. (redrawn from Tsukiji et al., 2018). F-G) Tracks from Gunbuk tracksite (Track 1A-5 and 2B-1).

Age estimation

When Xing et al. (2007) reported *C. lotus* ornithopod tracks from China, they subdivided them into three age groups according to track lengths: 37~40 cm (adults), 25~30 cm (subadults), and 19~23 cm (juveniles). In a similar way, Matsukawa et al. (1999) subdivided footprints that belong to *Caririchnium leonardii* from the Dakota Group (Albian-Cenomanian) into three age groups corresponding to track lengths: 29.3~55.0 cm (adults), 21.7~29.3 cm (subadults), and 16.5~21.7 cm (juveniles). Most of the Early Cretaceous ornithopod pes imprints found in Korea also range from 20 cm to 50 cm in length (Kim and Pickerill, 2003; Lockley et al., 2012c; Kim et al., 2016; Lee et al., 2018c). Interestingly, all pes tracks of the Gunbuk site do not exceed 27 cm in length, clearly indicating that they were made by the juvenile to subadult bipedal ornithopods.

Size and speed estimation

Several formulas are being used for estimation of size, locomotion speed, gait, and body length or mass of trackmakers from the measurements of the trackway. Since Alexander (1976) and Thulborn (1982) began studies about the locomotion in a statistical way from the trackway, these estimates were used as good proxies for the explanation of how trackmakers moved. The formulas used for the estimation are:

Hip height (h) ≈ 4.6L (small biped dinosaurs in general; Thulborn, 1989)

Relative stride length = SL/h (Alexander, 1976)

Locomotion speed (v) ≈ $0.25g^{0.5}SL^{1.67}h^{-1.17}$ (Alexander, 1976)

Thulborn (1989) suggested different estimation of hip height for different taxa, such as 4.8L for small ornithopods with foot length shorter than 25 cm, or $3.97L^{1.08}$ for small ornithopods, but this equation was obtained from allometric equations (Thulborn, 1984). In the case of Gunbuk tracksite, all trackmakers are considered as bipedal animals, so we chose the value of 4.6L for small biped dinosaurs in general. Relative stride length is used as a function of the Froude number, which applies to any situation where inertia and gravity interact and usually used in describing the motion of a fluid (Alexander, 1976). In the ichnological study of trackways, relative stride length is used to determine the gait of trackmaker. Mammals generally shift from a walk to a trot when relative stride length reaches about 2.0 and when it reaches 2.9 a trotting gait changes to running (Thulborn, 1982). These values have been used in other ichnotaxa as criteria for gait analysis. By following their formulas, hip heights of trackmakers of Gunbuk tracksite range from 76.4 cm and 102.1cm with an average of 89.1 cm. The relative stride lengths vary between 1.31 and 1.63, implying that all trackways are made by constant walking. Locomotion speed ranges from 4.0 km/h to 5.8 km/h (Table 2).

TABLE 2. Estimates of the trackways from the measurements.

Trackway	Hip Height (cm)	Relative Stride Length	Speed (m/s)	Speed (km/h)
1A	82.0	1.63	1.60	5.77
1B	76.4	1.46	1.28	4.62
2A	102.1	1.31	1.25	4.49
2B	96.3	1.53	1.57	5.63
2C	95.5	1.42	1.38	4.96
2D	82.2	1.31	1.12	4.02
Average	89.1	1.44	1.37	4.92

Locomotory pattern

Most of Gunbuk pes tracks show centered and developed digit III impressions with high AT l/w ratio, which is occasionally described to be ‘mesaxonic’ in purely geometric and dimensional terms (Lockley, 2009; Romano et al., 2020). Nonetheless, here we describe ‘axony’ in a functional term as an axis that receives the greatest load during locomotion (*sensu* Leonardi, 1987; Romano et al., 2020).

Gunbuk tracks generally show deeper impressions in the digits than the metatarsophalangeal impression, meaning that load was mostly supported by the digits. Some well-preserved tracks like track 1A-5 or 2B-1 (Figs. 10, 11) show deep impressions on digits II and III, implying that the load was mainly supported by the centro-medial part of the pes (entaxonic) during the maximum load phase. However, Track 1A-2 (Fig. 12) exhibit that digits III and IV are relatively deeply impressed than other parts of footprint, indicating the weight was supported by the centro-lateral part of the pes (ectaxonic) during the maximum load phase, showing opposite condition so that its locomotory pattern was not consistent even within one trackway from the point of view of maximum load phase (Lallensack et al., 2016; Razzolini et al., 2016). Moreover, in track 2B-3 (Fig. 13), only the distal part of digit III is more deeply impressed than other parts. Such an impression might not imply that the distal end of digit III is the only weight-bearing part of pes during the maximum load phase, but rather it might suggest that hindfoot of the trackmaker left centrally (mesaxonic) during the kick-off phase.

Juvenile gregarious behavior

The possible gregarious behavior of dinosaurs has been reported many times in forms of multiple (sub-) parallel trackways, the congregation of eggs and nests, or concentrated skeletons of a single or similar species (Ostrom, 1972; Horner and Makela, 1979; Currie, 1998, Kobayashi and Lü, 2003). There are many reports on multiple ornithopod trackways in the world, nevertheless, most of them were made by only adults or a mixed group of adults and juveniles (Carpenter, 1992; Zhang et al., 2006; Kim et al., 2009; Lockley et al., 2012c; Fiorillo et al., 2014; Xing et al., 2015, Piñuela et al., 2016). Although evidence of the juvenile communities had been reported among various dinosaur taxa such as ornithomimids, sauropods, and ceratopsians based on their body fossils (Varricchio et al., 2008; Myers and Fiorillo, 2009; Zhao et al., 2013), the ichnological evidence to prove is relatively rare in ornithopod dinosaurs.

Pérez-Lorente et al. (1997) reported three parallel small to medium-sized tridactyl trackways from the Les Cerradicas tracksite (Berriasian), Spain, and interpreted them as gregarious behavior, but the ichnotaxon and age of trackmakers are uncertain. On the other hand, sixteen multiple trackways of small ornithopods (*Caririchnium*) were discovered from the Mosquero Creek tracksite, Mesa Rica Formation (early Upper Cretaceous), New Mexico (Lockley and Hunt, 1995). These trackways were hypothesized as herding at first and later supported with their distribution of speed and direction as well as the relationship between track size and relative stride length (Cotton et al., 1998). In South Korea, at least six parallel trackways of small ornithopods (track length 12 ~ 15 cm) from the Upper Cretaceous Neungju Basin, South Jeolla Province were also interpreted as herding of small ornithopods (Lockley et al., 2012b).

Gunbuk trackways can be subdivided into four groups based on their orientations: Group 1 (Trackways 1A and 1B), Group 2 (Trackways 2A and 2C), Trackway 2B, and Trackway 2D. The average azimuths of groups 1 and 2 show the parallel orientation of two trackways (Table 1). Assuming that the lake shoreline did not dramatically change from the ripple azimuth of 120° on Layer A throughout the track-bearing horizons, Group 1 and Trackway 2B can be interpreted as moving side to side along the lake shoreline implying a herding of Group 1, while Group 2 might have moved away perpendicularly from the lake. Trackway 2D seems to be crossing Trackway 2B at an angle around 13°, and the former can be also interpreted as moving along the lake shoreline. All cases above support the hypothesis that juvenile ornithopods were gregarious and moved as independent clusters after hatching until they joined herds of more mature animals (Currie and Sarjeant, 1979; Currie, 1983).

Cotton et al. (1998) argued that ornithopod trackways from the Mosquero Creek, Dakota Group show an anticorrelation between footprint size and relative stride, indicating that smaller and larger animals reach similar locomotion speed as they move together. Trackway 1A shows bigger footprints and larger relative stride length than those of Trackway 1B, indicating that it simply walked faster. On the other hand, Trackway 2A shows bigger footprints but smaller relative stride length than Trackway 2C, suggesting slow walking to lower the gap of moving speed between two trackmakers (Table 2). Trackmakers of Trackway 2A and 2C were likely to be moving together, but the probability of simultaneous moving is lower in the case of 1A and 1B. Two trackmakers might have moved individually along the shoreline with a time gap between them. Trackway 2B and 2D might be also assumed as a herd, but 2B shows larger foot length with larger relative stride length. Moreover, the difference between the two azimuth angles is larger than any other group. These two trackways would be similar to the relation between Trackway 1A and 1B. However, the trackway lengths at Gunbuk tracksite are too short to achieve statistical significance, thereby this conclusion is tentative.

CONCLUSIONS

The Gunbuk tracksite provides a window into the Early Cretaceous ornithopod community that lived in a marginal lacustrine environment. Based on the footprint size and morphological characteristics, all tracks belong to juveniles or subadults of derived iguanodonts or basal hadrosauroids, and are assigned to the ichnogenus *Caririchnium*. Trackways generally show preferred orientations in subparallel directions, implying gregarious behavior of juvenile ornithopods moved along the lake shoreline. The total absence of adult footprints on three track-bearing horizons suggest that juvenile ornithopods made sometimes juvenile-only clusters and moved spatially separated from adult groups.

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APPENDIX 1. Measurements of tracks and trackways from Layer 1

Trackway	#	L	W	L/W	II	III	IV	D(II-III)	D(III-IV)
1A	1	16.0	16.8	0.95	10.8	16.0	14.2	31.3	31.9
	2	17.7	16.8	1.05	13.4	17.7	16.0	29.4	30.1
	3	-	-	-	-	-	-	-	-
	4	-	-	-	-	-	-	-	-
	5	19.8	17.3	1.14	13.8	19.8	15.1	28.8	32.1
1B	1	14.1	15.4	0.92	8.9	14.1	10.6	46.5	41.5
	2	-	-	-	-	-	-	-	-
	3	16.1	17.0	0.95	11.6	16.1	13.2	43.6	32.3
	4	16.9	15.5	1.09	14.9	16.9	13.3	28.0	25.9
	5	16.9	16.6	1.02	12.3	16.9	15.9	30.8	26.1
	6	19.0	17.4	1.09	15.8	19.0	14.9	31.9	27.8
Isolated	1	13.1	-	-	10.2	13.1	-	43.3	-
	2	-	-	-	19.0	-	-	-	-
	3	-	-	-	-	-	-	-	-
	4	-	-	-	-	-	-	-	-
	5	15.4	17.1	0.90	13.0	15.4	11.1	33.1	41.3
	6	16.0	14.3	1.12	12.8	16.0	13.5	21.9	27.9
	7	-	-	-	-	-	-	-	-
	8	17.9	17.8	1.01	14.7	17.9	12.3	25.4	31.8
	9	20.1	18.0	1.12	14.9	20.1	16.8	25.8	21.4
Average		16.8	16.7	1.03	13.3	16.8	13.9	32.3	30.8

Trackway	#	Azimuth	SL	PL	ANG	TR	ATl	ATw	AT l/w
1A	1	140.8	131.2	64.4	-	1.4	5.4	13.4	0.40
	2	151.3	137.5	69.4	158.1	9.0	5.0	14.7	0.34
	3	-	132.6	69.4	164.3	-	-	-	-
	4	-	-	65.9	157.3	-	10.1	13.4	0.75
	5	138.1	-	-	-	4.1	7.4	14.7	0.50
1B	1	141.4	118.0	57.6	-	0.6	7.0	13.7	0.51
	2	-	110.4	61.1	167.7	-	4.6	16.8	0.27
	3	140.6	106.2	50.6	163.5	0.2	6.1	15.3	0.40
	4	138.9	110.4	57.3	166.4	1.9	4.5	12.8	0.35
	5	143.8	-	55.0	159.2	3.0	4.4	13.8	0.32
	6	142.2	-	-	-	1.4	5.7	15.2	0.38
Isolated	1	152.6	-	-	-	-	-	-	-
	2	-	-	-	-	-	-	-	-
	3	-	-	-	-	-	5.1	13.7	0.37
	4	-	-	-	-	-	-	-	-
	5	139.8	-	-	-	-	5.7	14.5	0.39
	6	223.9	-	-	-	-	4.0	10.7	0.37
	7	-	-	-	-	-	-	-	-
	8	343.5	-	-	-	-	5.8	13.1	0.44
	9	56.9					5.4	13.0	0.42
Average		-	-	-	-	-	5.7	13.9	0.42

APPENDIX 2. Measurements of tracks and trackways from Layer 2

Trackway	#	L	W	L/W	II	III	IV	D(II-III)	D(III-IV)
2A	1	20.4	21.6	0.94	16.6	20.4	14.7	32.5	35.6
	2	22.1	19.1	1.16	13.3	22.1	15.7	31.7	30.4
	3	20.9	-	-	16.1	20.9	-	23.7	-
	4	25.4	-	-	-	25.4	21.1	-	21.8
2B	1	22.5	18.2	1.24	18.1	22.5	17.3	22.0	28.6
	2	20.0	17.3	1.16	14.4	20.0	17.2	31.4	22.5
	3	20.6	18.8	1.10	16.1	20.6	15.6	25.4	32.4
	4	20.6	16.9	1.22	14.9	20.6	18.1	26.6	22.9
2C	1	21.3	-	-	-	21.3	16.5	-	26.7
	2	20.2	17.7	1.14	17.8	20.2	15.5	18.6	30.1
	3	20.8	-	-	17.2	20.8	-	21.5	-
2D	1	19.2	15.7	1.22	14.5	19.2	14.3	26.7	28.8
	2	16.4	16.3	1.01	13.2	16.4	13.5	37.0	31.1
	3	-	-	-	-	-	-	-	-
	4	-	16.4	-	-	-	-	-	-
	5	18.0	15.7	1.15	14.6	18.0	13.1	28.1	34.8
	6	-	-	-	-	-	-	-	-
Isolated	1	14.6	16.4	0.89	10.9	14.6	10.7	35.5	38.9
	2	19.7			16.6	19.7		28.1	
	3	23.2	18.2	1.27	17.6	23.1	16.3	22.2	31.1
	4	21.7			16.6	21.7		26.9	
	5	-	-	-	-	-	-	-	-
	6	16.0	15.3	1.05	12.5	16.0	11.7	32.5	33.6
	7	21.0	16.1	1.30	18.6	21.0	15.8	24.1	23.8
	8	22.4	23.8	0.94	18.4	22.4	18.9	31.0	37.7
	9	20.0	19.9	1.01	14.9	20.0	18.2	34.8	31.1
	10	21.8	21.4	1.02	18.4	21.8	18.7	30.5	33.8
	11	18.8	18.9	0.99	15.6	18.8	14.1	26.5	41.2
	12	26.8	26.3	1.02	25.2	26.8	20.1	20.4	32.3
Average		20.6	18.5	1.10	16.2	20.6	16.1	27.7	30.9

Trackway	#	Azimuth	SL	PL	ANG	TR	ATl	ATw	AT l/w
2A	1	38.1	134.3	68.5	-	5.6	7.3	17.6	0.41
	2	23.6	133.9	65.9	179.1	8.9	9.5	15.2	0.63
	3	44.5	-	68.4	176.0	12.4	-	-	-
	4	27.0	-	-	-	5.5	-	-	-
2B	1	104.1	149.4	77.6		28.3	6.4	15.1	0.42
	2	132.1	145.5	72.1	175.8	0.4	5.8	14.5	0.40
	3	122.3	-	73.6	178.2	10.1	6.6	15.3	0.43
	4	136.5	-	-	-	4.0	5.5	14.1	0.39
2C	1	38.1	135.9	68.4	-	8.3	-	-	-
	2	26.1	-	67.6	174.5	3.7	4.5	14.0	0.32
	3	54.5	-	-	-	24.7	-	-	-
2D	1	125.9	103.6	55.0		10.6	6.4	13.5	0.47
	2	160.1	105.9	48.9	171.6	23.6	5.3	15.0	0.35
	3	-	109.9	57.0	179.9	-	5.6	15.7	0.36
	4	-	112.0	53.1	173.1	-	5.6	13.9	0.40
	5	123.4		59.0	175.1	13.1	6.1	14.5	0.42
	6	-	-	-	-	-	6.4	15.3	0.42
Isolated	1	128.4	-	-	-	-	6.0	13.0	0.46
	2	132.1	-	-	-	-	-	-	-
	3	118.7	-	-	-	-	7.7	15.2	0.51
	4	122.4	-	-	-	-	-	-	-
	5	-	-	-	-	-	-	-	-
	6	150.4	-	-	-	-	5.9	13.3	0.44
	7	123.6	-	-	-	-	5.3	14.2	0.37
	8	347.5	-	-	-	-	7.0	20.1	0.35
	9	155.5	-	-	-	-	6.0	18.2	0.33
	10	140.5	-	-	-	-	6.1	19.8	0.31
	11	123.2	-	-	-	-	6.2	16.6	0.37
	12	136.5	-	-	-	-	5.5	20.9	0.26
Average		-	-	-	-	-	6.2	15.7	0.40

APPENDIX 3. Measurements of the tracks from Layer 3

Trackway	#	L	W	L/W	II	III	IV	D(II-III)	D(III-IV)
Isolated	1	16.4	13.8	1.19	11.0	16.4	10.3	31.1	31.6
	2	13.6	12.5	1.09	11.2	13.6	10.2	23.4	33.4
	3	15.3	9.5	1.61	9.2	15.3	10.7	15.7	20.2
	4	14.3	-	-	11.5	14.3	-	28.4	-
	5	16.7	16.4	1.02	11.9	16.7	11.3	44.9	38.9
	6	12.9	12.0	1.08	9.7	12.9	10.9	29.2	26.3
Average		14.9	12.8	1.20	10.8	14.9	10.7	28.8	30.1
Trackway	**#**	**SL**	**PL**	**ANG**	**TR**	**ATl**	**ATw**	**AT l/w**	**Azimuth**
Isolated	1	-	-	-	-	7.3	11.1	0.66	117.5
	2	-	-	-	-	4.1	10.2	0.40	60.1
	3	-	-	-	-	5.8	6.3	0.92	51.7
	4	-	-	-	-	-	-	-	123.9
	5	-	-	-	-	8.0	15.5	0.52	109.9
	6	-	-	-	-	3.7	9.6	0.39	118.9
Average		-	-	-	-	5.8	10.5	0.58	-

국문초록

2018 년 경상남도 함안군 군북면의 하부 백악기(알브절)에 해당하는 함안층에서 비성체 조각류 공룡 발자국 화석지가 새롭게 발견되었다. 화석지($33\ m^2$)의 작은 개울가 바닥에 부분적으로 노출된 3 개의 층준에서 55 개의 조각류 발자국(6 개의 짧은 보행렬과 보행렬을 알 수 없는 27 개의 발자국)이 관찰되었다. 발자국이 발견되는 층준과 그 상위 층에서 나타나는 암상과 퇴적구조를 바탕으로 당시 퇴적층은 호수주변부 환경에서 퇴적되었을 것으로 추정하였다. 발자국은 모두 발가락이 3 개이고, 준대칭적인 형태를 띠는 소-중형의 뒷발자국이다. 모든 발자국들은 짧고 넓으며 뭉툭한 발가락 자국과 크고 둥근 형태의 발꿈치 자국을 갖고 있다. 앞발자국은 발견되지 않았다. 발자국들은 전반적으로 좌우 너비보다 앞뒤로 길고, 중지 발가락(3 번째 발가락)이 뚜렷하게 발달한 형태를 보인다. 보행렬에서 나타나는 발자국들의 방향은 보행렬 안쪽을 향하고 있다. 발자국의 형태적인 특징으로 보아 군북 화석지의 발자국들은 생흔속 카리리크니움(*Caririchnium*)에 속할 가능성이 가장 높다. 동시기 한국에 살았던 대형 조각류 공룡들과 비교해 보았을 때, 상대적으로 작은 뒷발자국의 크기(13 ~ 27 cm)는 발자국을 남긴 공룡들이 아성체에서 준성체에 해당하는 조각류였음을 지시한다. 각 층준에서 발견되는 보행렬은 대부분 거의 평행한 그룹으로 묶여 특정 방향으로 진행하는 경향을 보여주며, 이로부터 이들이

군집생활을 하였음을 추정할 수 있다. 특히, 본 화석지에서는 오직 어린 조각류 개체들의 발자국만 발견되는데, 이는 다양한 연령대의 발자국이 발견되거나 대형 조각류의 발자국만 발견되는 대부분의 조각류 발자국 화석지와 다른 현상이다. 화석지 전체에 걸쳐 성체 발자국이 전혀 발견되지 않는 점은 그 당시 조각류 개체군이 연령에 따라 공간적으로 분리되었고 이에 따라 성체의 보살핌을 받지 않는 어린 개체들만으로도 군집을 형성하였던 것으로 해석할 수 있다.

주요어: 발자국, 카리리크니움(*Caririchnium*), 아성체 공룡, 조각류, 전기 백악기, 함안층, 함안군, 대한민국

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